THE TRICHOMES OF THE GOODENIACEAE

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Synopsis

A survey of trichomes in the Goodeniaceae is reported. It is concluded that there are seven distinct types of trichome: (1) stellate-simple; (2) uniseriate multicellular; (3) branched multicellular; (4) T-shaped; (5) glandular; (6) dendritic; (7) Brunonia-type. Types (1), (5) and (6) are subdivided into subtypes. Each type is morphologically distinct and therefore has had a long, separate evolutionary history. The hair types confirm previous suggestions in systematic rearrangement and again call into question the groupings made by the most recent monographer (Krause).

Introduction

The trichomes of the Goodeniaceae have not been examined in detail before. Krause (1912) makes passing references to them in his introductory paragraphs but gives few illustrations. He uses the indumentum type in his species descriptions and keys but only distinguishes between glandular, stellate and simple types, and in *Dampiera* provides some illustrations of different sorts of dendritic hairs. In some cases he refers to a species as being glabrous when, in fact, it does have numerous microscopic hairs (e.g. *G. ovata*). Colloza (1907, 1908) mentions the trichomes in a very few cases and illustrates only those of *Brunonia*. Hummel (1962) does not appear to mention the family.

The use of trichomes in taxonomic studies is well established by a long line of investigators, particularly in the family Gramineae. In other families the taxonomist is usually content to describe the macroscopic appearance and texture of the indumentum. Uphof (1962) draws attention to a few cases in which more detailed investigations have been carried out. It is primarily because of their potential use in the taxonomy of the family that the present investigation has been undertaken.

Material and Methods

Most of the observations have been carried out on herbarium material. Thin, surface sections of the dry material were cut by hand with a sharp razor blade; the section bleached and soaked in a mixture of commercial bleaching agent and weak detergent. The sections were then mounted in Gurr's water-mounting medium without staining. In the few cases where fresh material was available the soaking in the bleach was omitted. In addition, transverse sections of the leaves and corollas were prepared by embedding in paraffin wax in the usual manner. These two sets of preparations were further supplemented by observations on the whole specimen, scraping the hairs off the epidermis with a razor blade and mounting in Gurr's water-mounting medium.

Some of the sections were stained to distinguish the cuticle; the stains used were ammoniacal fuchsin and Auromine. The former stains the cuticle red and also shows a brilliant fluorescence, whilst the latter is visible only with fluorescence microscopy.

Observations

Coopernookia : Three basically different types of trichomes are found in this genus. Uniseriate multicellular hairs (Fig. 5) are almost restricted to the leaf axil. They consist of a basal cell with a prominent cuticle and a varying number of other cells with thin walls and a cuticle that is only visible using fluorescence microscopy. The so-called stellate hairs (Carolin, 1968) consist of a basal group of cells without outgrowths but with heavily cutinized surfaces, surmounted by a series of thick-walled, thin-cuticled cells with long, stiff, pointed outgrowths (Fig. 1, F). Furthermore, there are glandular hairs present and, whilst the two former hair-types are more or less uniform throughout the genus, these latter show some variation. In *C. barbata* the head of the hair is unicellular (Fig. 6). *C. chisholmii* also has this form of glandular hair but they are much less frequent. In *C. strophiolata*, *C. polygalacea* and *C. georgei* the head is four-celled and so flattened as to appear almost peltate (Fig. 3, E).

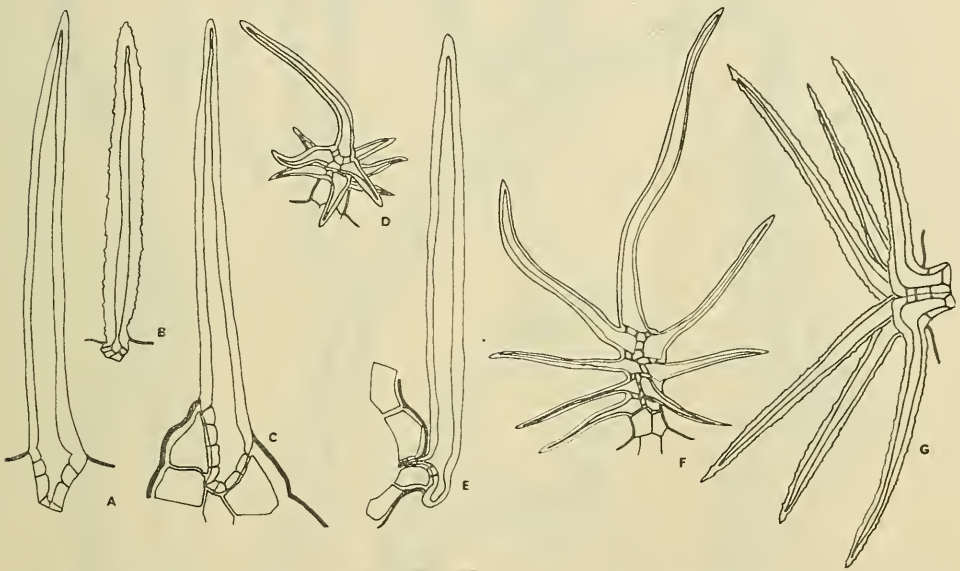

Fig. 1. Stellate and simple hairs. A. *Goodenia ovata*. B. *Diaspasis filifolia*. C. *Goodenia pinnatifida*. D. *Goodenia stelligera*. E. *Goodenia subintegra*. F. *Coopernookia polygalacea*. G. *Scaevola tomentosa*.

Velleia : Only simple unicellular hairs are found in this genus, except for some uniseriate multicellular hairs in the leaf axils. The former have thick cell walls which extend down into the basal part ; the cuticle is very thin, and scarcely visible using normal staining and lighting. The only variation in the microscopic form of the hairs is in the degree to which the surrounding epidermal cells are raised up into a sheath around the base of the hair. This is fairly conspicuous in *V. hispida* (as in Fig. 1, C) but much less so in *V. paradoxa* and *V. trinervis* with *V. rosea* and *V. daviesii* showing intermediate conditions. Indeed, the size of the sheath is variable in the one species to some extent, although *V. hispida* in particular shows a constantly well-developed sheath.

Goodenia : This large genus displays a wide variety of trichomes ; most species have tufts, however minute, of uniseriate multicellular hairs in the leaf axils ; it is, however, the surface trichomes to which we should divert attention.

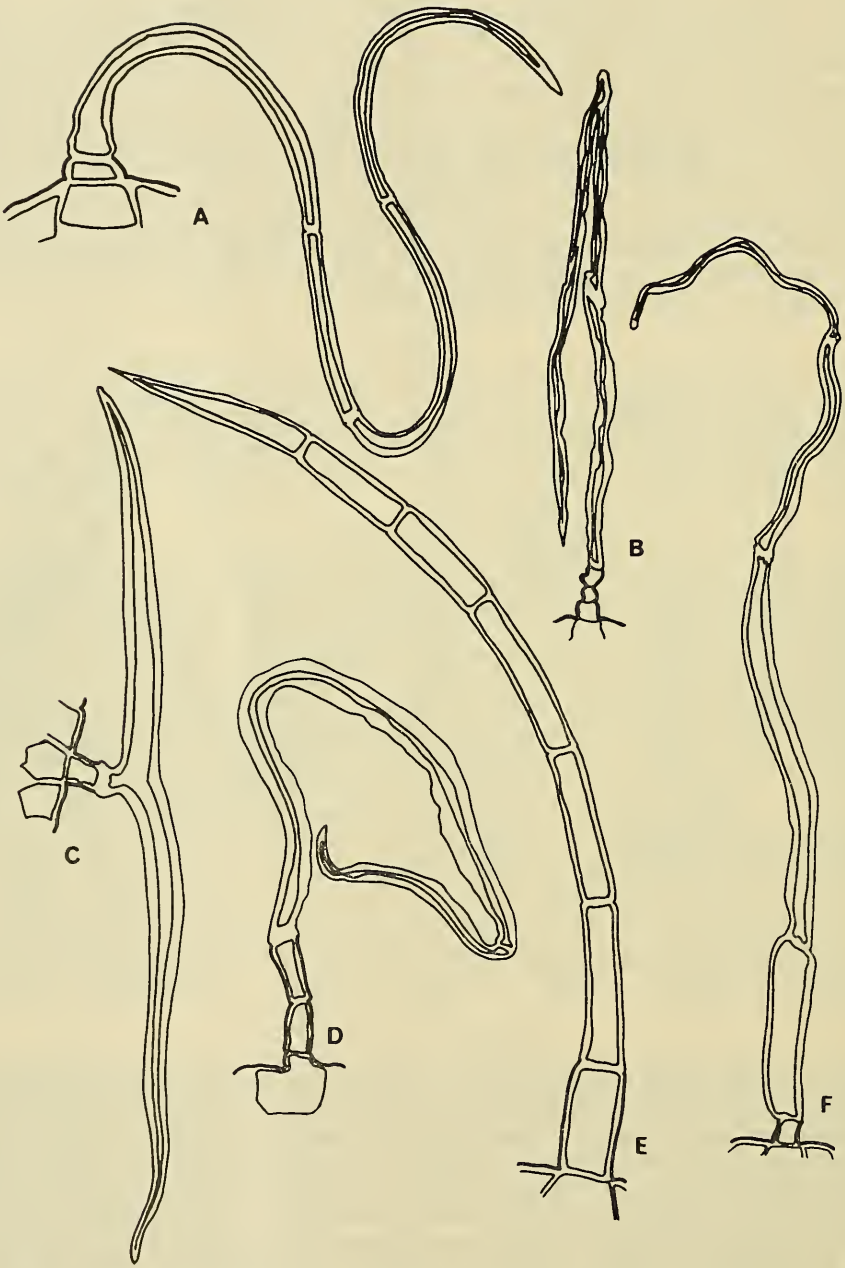

Fig. 2. Uniseriate multicellular and T-shaped hairs. A. *Goodenia incana*. B. *Goodenia hederacea*. C. *Goodenia mueckeana*. D. *Goodenia primulacea*. E. *Pentaptilon careyi*. F. *Goodenia heterochila*.

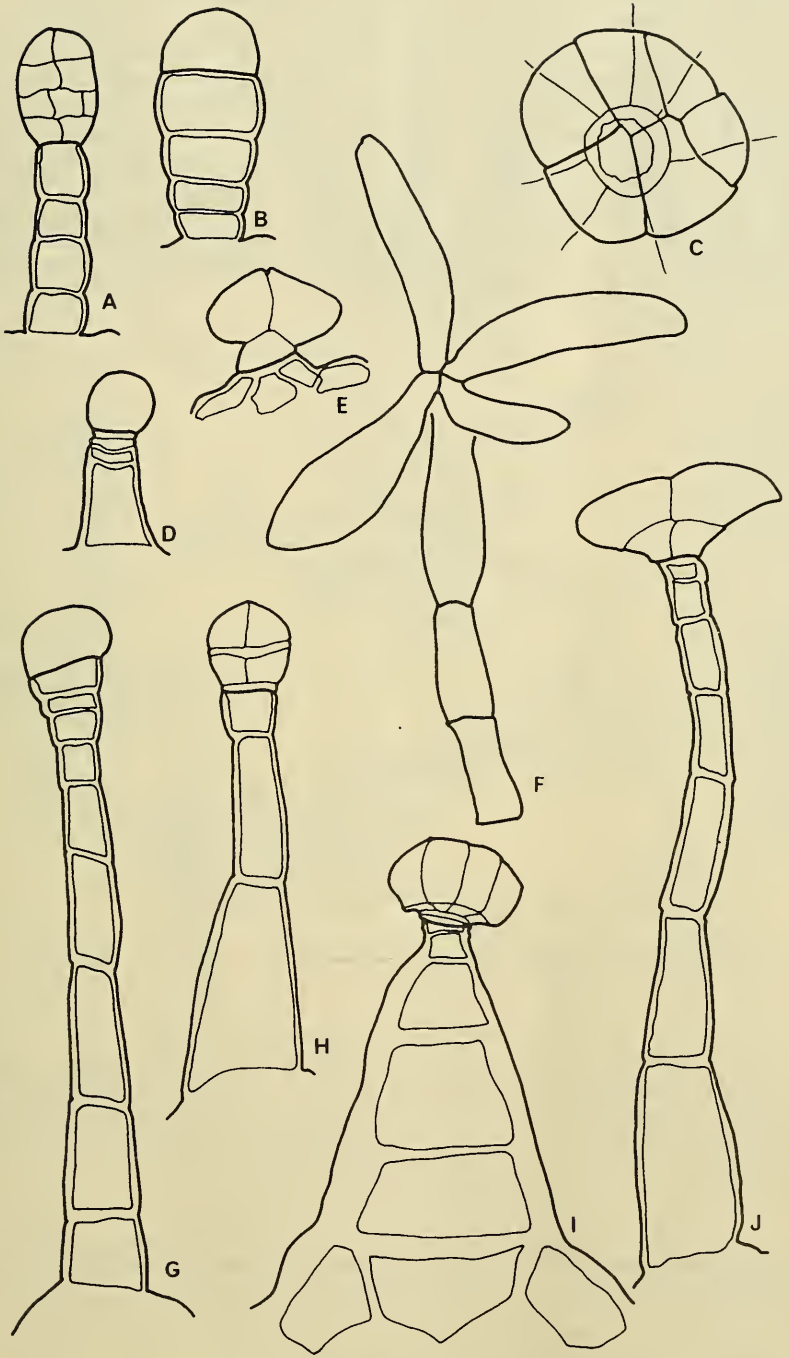

Fig. 3. Glandular hairs. A. *Calogyne* sp. B. *Goodenia decurrens*. C. *Goodenia ovata*. D. *Goodenia concinna*. E. *Coopernookia polygalacea*. F. *Scaevola coriacea*. G. *Goodenia stephensonii*. H. *Pentaptilon careyi*. I. *Goodenia barilletii*. J. *Leschenaultia hirsuta*.

Despite the inadequacies of Krause's (1912) treatment (see Carolin, 1959, 1968), it seems best to use this as a basis for reporting these findings.

The various forms of the trichomes are shown in Figs. 1, 2 and 3, and Table 1 indicates their occurrence in the species examined. The stellate type is virtually the same, although generally shorter, as the stellate type in *Coopernookia.* Submerged stellate can be looked upon as the stellate type which has lost the basal column of more heavily cutinized cells, or as a cluster of simple trichomes. The simple and ensheathed simple trichomes have the same form as those found in *Velleia.* The one-sided simple hairs appear to be unique to *Goodenia* ; these hairs are appressed and apparently ensheathed on one side, but this is obscured by an outgrowth of the trichome more or less overlapping and obscuring the basal sheath (Fig. 1, E). *G. mueckeana* appears to have a unique form of simple hair in that it is T-shaped (Fig. 2, C).

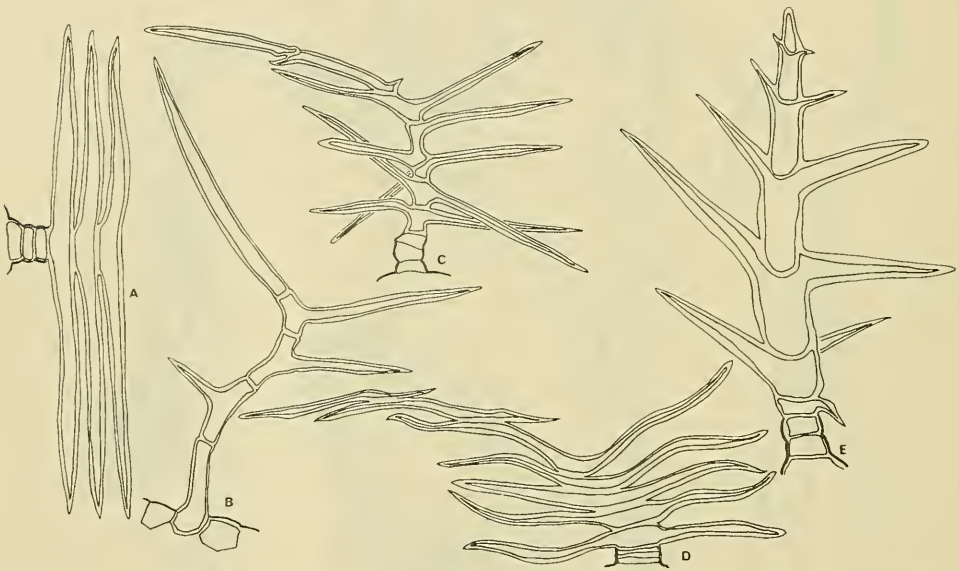

Fig. 4. Dendritic hairs and branched multicellular hairs. A. *Dampiera coronata.* B. *Verrauxia reinwardtii.* C. *Dampiera tomentosa.* D. *Dampiera stricta.* E. *Dampiera purpurea.*

The glandular hairs can be divided into those with a single-celled head and those with a multicellular head (Fig. 3, A-E). In a few multicellular headed hairs the head is flattened to give the peltate hair (Fig. 3, C), but in others the the number of tiers of cells in the head is multiplied considerably and the head is oval or spherical in shape. This latter type may have a stalk which is uniseriate to the base (Fig. 3, A) or multicellular at the base (Fig. 3, I).

Calogyne: This genus falls into two fairly well defined groups on the basis of hair type, although at first they appear similar in that both have glandular and simple hairs.

C. berardiana has simple hairs more or less ensheathed on one side only (as in Fig. 1, E) and glandular hairs with single-celled heads.

C. holtziana and *C. purpurascens* have simple, practically sheathless cells and glandular hairs with multicellular heads (Fig. 6, V, 2).

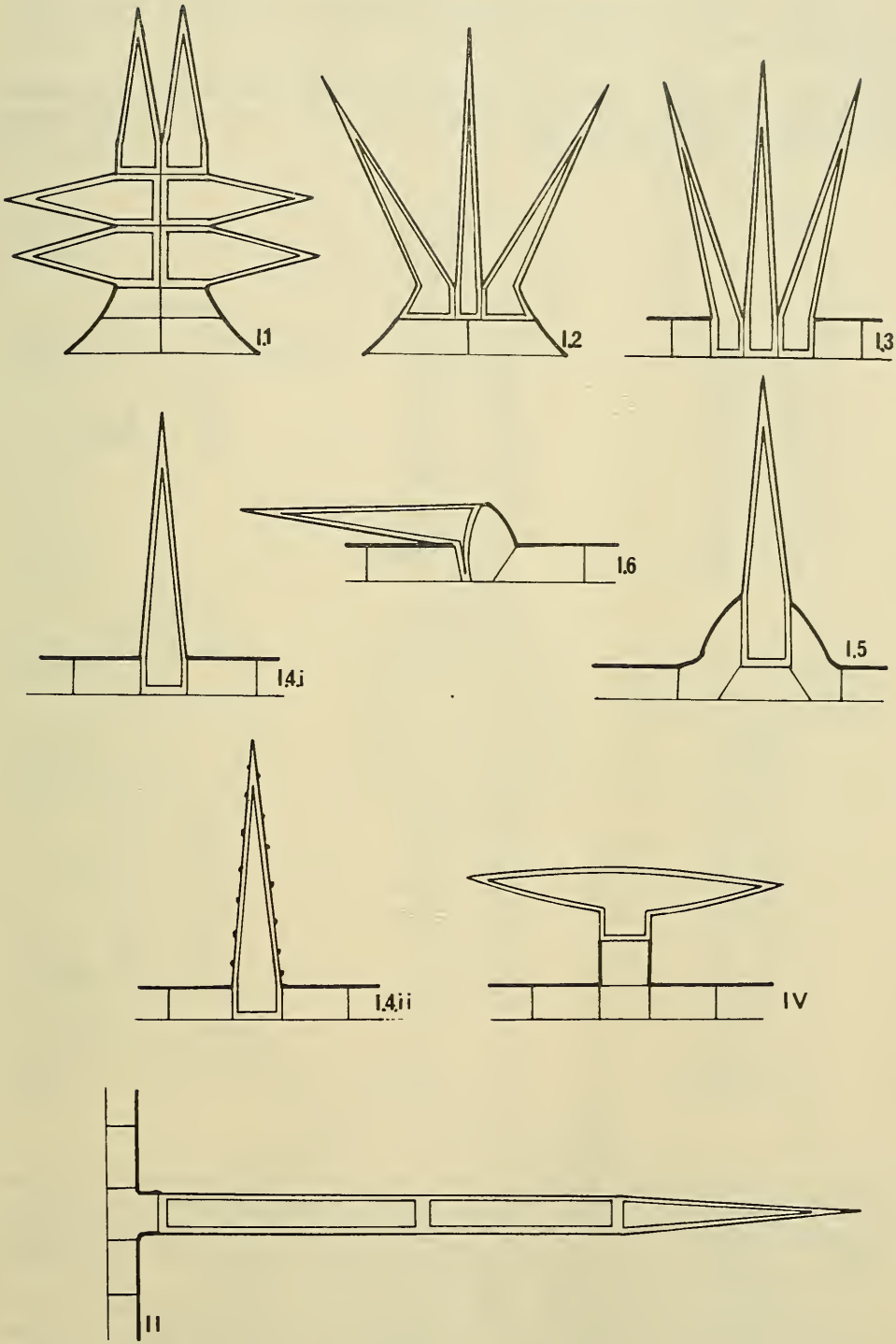

Fig. 5. Hair types, see Table III.

Catosperma: The single species *C. goodeniaceum* has a few short simple hairs, particularly on the sepals, and rather more numerous cottony, multicellular hairs.

Diaspasis: The single species *D. filiformis* has very thick-walled unsheathed simple hairs in which the cuticle is raised into numerous warty outgrowths; the wall is conspicuously striated.

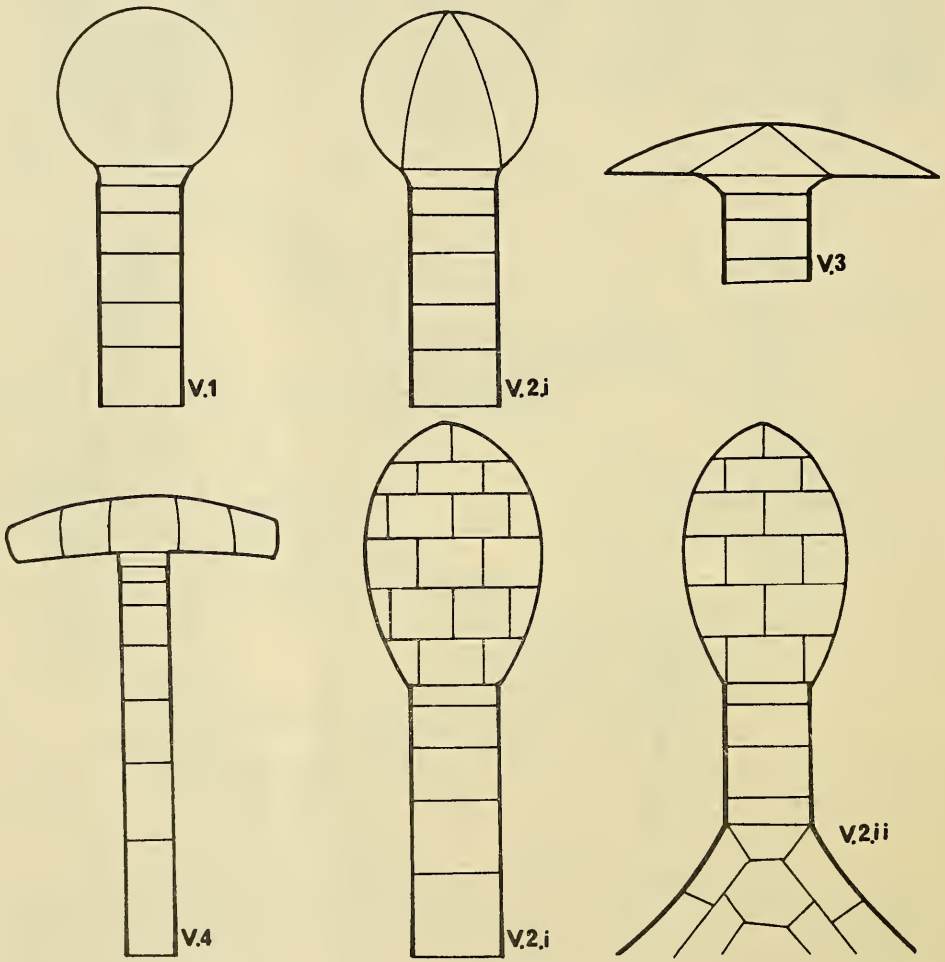

Fig. 6. Hair types, see Table III.

Scaevola: This genus shows rather fewer hair types than the other large genus *Goodenia*. In fact, however, another subtype is found which is almost a characteristic feature of the genus, i.e. the simple hair with an uneven, warty surface (Fig. 1, B). The occurrence of hair types in *Scaevola* and its supposed relative *Diaspasis* is shown in Table 2.

It can be seen from this that stellate hairs are very infrequent, found only in *S. tomentosa* (Fig. 1, G) of the species examined. Simple, smooth hairs are also rare, being found only in *S. mollis*. The glandular and peltate types have apparently the same construction as those of *Goodenia*.

TABLE 1
Distribution of Hair Type in Goodenia *and Related Genera*

Name	Stellate I.1 and I.2	Submerged Stellate I.3	Simple I.4.i	En-sheathed Simple I.5.i	One-sided Simple I.6	Multi-cellular II	T-shaped IV	Glandular V.1	Glandular with Multi-cellular Head V.2.i	Glandular with Multi-cellular Head and Multi-cellular Base V.2.ii	Peltate V.3
GOODENIA											
Sect. Monochila											
G. viscida R.Br.											
G. xanthotricha De Vriese											
G. watsonii F. Muell.											
G. sericostachys Gardner											
Ser. Racemosae											
G. quadriloculoris R.Br.											
G. eremophila E. Pritzel											
G. stapfiana Krause											
G. ramellii F. Muell.											
G. decurrens R.Br.											
G. bellidifolia Sm.						+					
G. stelligera R.Br.						+					
G. rostrivalvis Domin						+		+			
G. dimorpha Maiden et Betche											
G. geniculata R.Br.											
G. primulacea Schlechtd.											
G. robusta (Benth.) Krause						+					
G. affinis De Vriese											
G. heterophylla Sm.			+					+			
G. hederacea Sm.											
G. rotundifolia R.Br.			+			(+)					
Ser. Suffruticosae											
G. ovata Sm.			(+)								
G. varia R.Br.											
G. macleana F. Muell.											
G. amplexans F. Muell.			+					+			
Ser. Coeruleae											
G. azurea F. Muell.			(+)								
G. incana R.Br.											
G. horniana F. Muell. et Tate			+					+	+		
G. scaevolina F. Muell.											
G. coerulea R.Br.			(+)								
G. trichophylla De Vriese ex Benth.											
Ser. Foliosae											
G. mitchellii Benth.											
G. heterochila F. Muell.								+			
G. hispida R.Br.											
G. grandiflora Sims											
G. chambersii F. Muell.								+			
G. macmillanii F. Muell.											
G. armstrongiana De Vriese				+							
Ser. Pedicellosae											
G. cycloptera R.Br.			+								
G. pinnatifida Schlechtd.											
G. pusilliflora F. Muell.				+							
G. elongata Labill.			+								
G. glauca F. Muell.											
G. subintegra F. Muell. ex Black											
G. lunata Black											
G. heteromera F. Muell.						+					
G. pilchella Benth.											
G. concinna Benth.											
G. micrantha Christ. et Ost.				+							
G. cirrifica F. Muell.											
G. viburnina F. Muell.											
Sect. Amphichila											
G. paniculata Sm.											
G. gracilis R.Br.											
G. pumilio R.Br.		+									
Incertae Sedis											
G. tenuiloba F. Muell.											
COOPERNOOKIA											
C. polygalacea (De Vriese) Carolin											
C. barbata (R.Br.) Carolin	+										
C. strophiolata (F. Muell.) Carolin	+										+
VELLEIA											
V. hispida Fitzg.											
V. paradoxa R.Br.											
V. trinervis Labill.											
V. rosea Sp. Moore											
V. daviesii F. Muell.				+							

Pentaptilon : This monospecific genus has very much the same indumentum as *Verreauxia*, all the same types of hair are present, simple, unbranched multicellular, branched multicellular, glandular with multicellular heads.

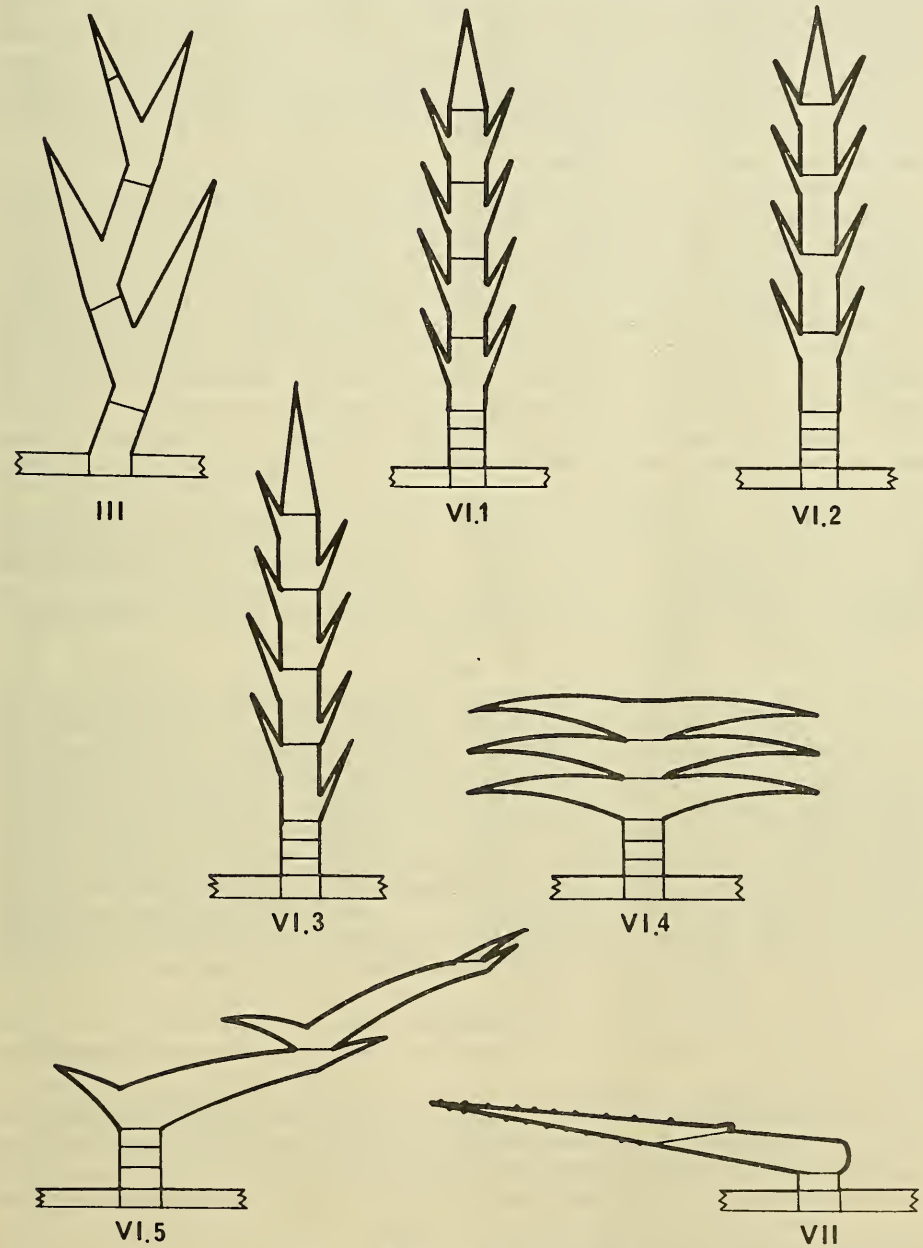

Fig. 7. Hair types, see Table III.

Leschenaultia : Few species of this genus appear to have trichomes except on the inner floral parts. *L. hirsuta* has glandular hairs with flattened multicellular heads on multicellular stalks. The heads are frequently knocked off and

consequently trichomes on the older parts of the plant often appear to be simple (Fig. 3, J).

Dampiera: This large genus appears to show only the dendritic hair-types These hairs at first sight appear to be similar to those of *Verreauxia* but differ in that they have two short arms instead of one to each cell, except the basal two or three and the terminal cell. There is some variation on the basic theme of this hair-type in *Dampiera* which will no doubt prove of taxonomic value in the future. The variation is concerned mainly with the position of the two branches of each cell with regard to each other, the length of the cells and the number of the cells in the trichome.

In *D. discolor* the arms are situated opposite each other and more or less in the middle of the cell (Fig. 7, VI.1), whilst in *D. hederacea*, *D. incana* and *D. luteiflora* they are situated at the top of the cell opposite each other (Figs. 4, E, 7, VI.2). In many species there is a tendency for the upper cells to be attached to the hair somewhat laterally rather than terminally on the preceding cell of the trichome, e.g. *D. spicigera* (Fig. 4, C). In *D. coronata*, *D. lindleyi* and *D. eriantha* there are only one to three armed cells, and the body of each cell is very short (Figs. 4, A ; 7, VI.4). There is a tendency also for each cell to be displaced laterally, as in *D. stricta* (which see) but this is usually very slight.

D. eriocephala and *D. adpressa* show the condition when the arms of each armed cell are not opposite but one is placed at the top of the cell and one at the bottom (Figs. 4, C ; 7, VI.3).

In *D. stricta* the arms are also displaced but, in addition, each succeeding cell of the trichome is bent horizontally at its base, thus giving a series of steps (Figs. 4, D ; 7, VI.5).

Brunonia: This genus has, at first sight, a hair-type entirely different from that found in any other genus in the family.

The hairs are multicellular and closely appressed to the epidermis. The basal cell is thin-walled and quite obviously cutinized, whilst all the succeeding cells are very thick-walled with a very thin cuticle. The first of these latter cells turns the trichome through 90° since it is attached horizontally to the basal cell (Fig. 7, VII). Moreover, it has a prominent groove in the upper surface, particularly towards the base. The next cell of the trichome is attached diagonally to the apex of the first and frequently the two spiral around each other for some distance (Fig. 7, VII). There are two subtypes, both found on the same plants. In one this second cell is the terminating cell and has large warty projections on the surface. In the second subtype, which is much longer, there are usually still more cells in the file, all attached to each other in much the same manner as indicated above, and none of them has prominent warty projections.

Discussion

On the basis of these results it is possible to distinguish seven main trichome types :

(i) Stellate-simple type in which one or several unbranched cells are arranged side by side in short multicellular files (Fig. 5, I.1–I.5).

(ii) Uniseriate multicellular type (Fig. 5, II).

(iii) Branched multicellular type in which each cell, except the basal and terminal ones, branch once (Fig. 7, III).

(iv) T-shaped type (Fig. 5, IV).

(v) Glandular type (Fig. 6).

(vi) Dendritic type in which each cell except some basal ones and sometimes the terminal one has two side-arms (Fig. 7, VI.1–VI.5).

(vii) *Brunonia*-type (Fig. 7, VII), which may be a derivative of (ii).

Each of these trichome types appears to have had its own independent phylogenetic history within the family ; independent that is, as far as any part of the organism can be independent of any other part. There is, moreover, probably no significant phylogenetic link between the main types, i.e., we cannot look upon any of the seven types outlined above as being derived from each other, with the possible exception of the *Brunonia*-type. They all differ from each other fairly significantly. For instance, it is improbable that the thick-walled stellate-simple trichome of horizontally arranged cells gave rise to the single-file multicellular hair or to the thin-walled secretory glandular hairs.

The dendritic type does show some similarity to the unbranched multicellular type in that they both consist of uniseriate files of cells with a basal group of heavily cutinized cells. It is felt, however, that any such derivation must have occurred at a very early stage in the history of the family since their appearances are now so different. There is a slight resemblance to the branched multicellular type, but this would appear to be rather superficial since there are no basal cells more heavily cutinized than the upper ones ; in fact, the insertion of these basal cells on the epidermis is more like that of simple hairs.

The most complex of the stellate-simple type is found in *Coopernookia* (Fig. 5, I.1). It has been indicated previously that this genus has a number of features that may be considered primitive in the genus (Carolin, 1966). This is really the only evidence that is available for suggesting a phylogenetic starting point for the various forms of this trichome type. It is easy enough to arrange these types in a series (Fig. 5), but to determine whether it is a reduction series or compounding series other evidence is necessary. For the reason given it will be considered as a reduction series in which first the individual units are contracted into a submerged, unilayered, stellate form (I.2) then submerged in the epidermis (I.3) and then reduced to a single unit forming a simple trichome (I.4). Type I.5 is similar but is ensheathed at the base by a raised plinth of cells.

The appressed hairs of *Goodenia glauca* and its allies are derived from the simple form by the excessive growth of the plinth cells on one side (I.6). The warty type might almost be considered a subform of the simple trichome. In many ways the T-shaped trichomes of *G. mueckeana* (Fig. 5, IV) could be mistaken for suppressed dendritic trichomes. However, it does not have the full complement of basal cells for the dendritic type. Furthermore, this latter type is completely unknown in *Goodenia*, to which *G. mueckeana* undoubtedly belongs, or any of its close relatives. If, in fact, this trichome type is genetically related to the dendritic type, it is either a phylogenetic " throw-back " of some significance or a feature which has been retained from the ancestral Goodeniaceae in only this one species over a very considerable period of time. In the absence of any further evidence probably the best course is to recognize it as a separate type. The presence of a basal cutinized cell may link this cell type to the unbranched multicellular type.

The unbranched multicellular type shows relatively little variation in form throughout those genera in which it occurs. The variation that does occur is confined to differences in length and straightness of the hair, features possibly significant taxonomically but not particularly so in a general survey of the type being reported here.

The dendritic type shows almost as much formal variation as the stellate-simple type. Again, it is almost impossible to decide which form is primitive ; possibly the equal-armed type with the arms at the mid-point of the cell could be taken as a starting point (Fig. 7, VI.1). Changes have been firstly the arms occurring at the top of each cell (Fig. 7, VI.2) and secondly one arm occurring at the top and one at the bottom (Fig. 7, VI.3). The suppression of the lower

part of each cell and the extension of the arms leads to Fig. 7, VI.5, whilst VI.5 has lead to form VI.6 by the whole trichome becoming appressed.

The *Brunonia* type could have been derived from this last form, i.e., 6, by suppression of both arms or their connation, or from type II. The evidence available does not allow a decision to be made.

Again, the glandular hair-type shows very considerable variation, and whilst it is easy enough to draw a series, the designation of the primitive condition is not so simple. Since the stalk is a file of cells, it seems reasonable to conclude that in the primitive condition the head will continue this sequence and also be unicellular. Thus this series can be looked upon as a compounding series, the head increasing in complexity. The first step is a double division of the terminal cell to give the situation in 2. In one line of change this becomes flattened into the peltate form of 3 and in another the multicellular form of 4 (all Fig. 6). The subforms of V.2 are based on the single or multicellular base. The form found in *Leschenaultia* is sub-peltate but with a long stalk.

Any sort of overall concept of evolution within the family must await more complete evidence. This survey of trichome form and phylogeny is an attempt to determine the homologies of the various trichomes, a task which has to be performed before any overall taxonomic or phylogenetic assessment can be made.

Functionally, it is possible that all these trichomes have a bearing on the adaption of these plants to the hot, dry, sunny climates in which many of them live. The non-glandular trichomes reflect incident light and heat and thus may restrict water loss. Various species have developed the appressed habit of trichomes, but using different types, thus in *Goodenia glauca* they are simple, in *Goodenia hederacea* they are uniseriate multicellular, in *Dampiera stricta* and *D. coronata* they are still another type ; the same apparent condition is achieved by non-homologous structures in these cases.

The glandular hairs may likewise function in decreasing water loss since they secrete a resin which covers the epidermis and frequently even obstructs the stomata.

More information is obviously necessary with regard to the physiology of these plants, but it is reasonable to assume that the trichomes do, in fact, have a significance in the adaptation of these organisms.

It seems clear that these trichomes will be important taxonomic characters. The last monograph of the family (Krause, 1912) made relatively little use of them.

In some ways this investigation indicates that adjustments may be needed in previous suggestions (Carolin, 1959, 1966, 1967 ; Peacock, 1963), although they promise to be relatively minor.

Verreauxia and *Pentaptilon*, otherwise clearly agreeing with *Goodenia* and its satellite genera, stand apart in their possession of branched multicellular hairs. *Leschenaultia*, likewise, shows an aberrant trichome type resembling those of the *Goodenia* group more than those of the *Dampiera* group.

On the other hand the trichome types of *Coopernookia*, *Goodenia*, *Velleia*, *Scaevola*, *Diaspasis*, *Catosperma* and *Calogyne* are all very similar and, apart from the presence of branched multicellular types, those of *Verreauxia* and *Pentaptilon* are also similar to those of *Goodenia*. This 7- and 8-chromosome group (Peacock, 1963), with " polytelic " inflorescences (Carolin, 1967), " Goodenioid " floral morphology (Carolin, 1959) and with a single ovular strand and frequently winged seeds (Carolin, 1966) has distinct similarities when the trichomes are considered. *Diaspasis* is clearly very close to *Scaevola* in its trichome type.

The other genera, in the 9-chromosome group (Peacock, 1963), are less similar, as indeed has been shown in other previous studies (Carolin, 1959, 1966.)

The trichomes of *Brunonia* may show certain similarities with those of *Dampiera* but they are not close (see above).

The trichome type also promises to be of some use in the subdivision of the larger genera, particularly in *Goodenia*, and less so in *Dampiera* and *Scaevola*. A glance at Table 1 will show the occurrence of multicellular hairs to be concentrated in the ser. *Rosulatae* and ser. *Racemosae* and peltate hairs occur in *G. ovata* and its relatives *G. vernicosa* and *G. varia*. The one-sided simple type likewise is concentrated in *G. glauca* and its relatives, whilst the other forms tend to be scattered.

Table 3

Refer to Figures. Standardized Hair Types in Goodeniaceae

Description	Type	Form	Subform	Figure
Stellate	I	1	i	5
Reduced stellate	I	2	i	5
Submerged stellate	I	3	i	5
Submerged stellate, warty surface	I	3	ii	
Simple	I	4	i	5
Simple, warty surface	I	4	ii	5
Ensheathed simple	I	5	i	5
Ensheathed simple, warty surface	I	5	ii	
One-sided simple	I	6	i	5
Multi-cellular unbranched	II	—	—	5
Multi-cellular branched	III	—	—	7
T-shaped	IV	—	—	5
Glandular	V	1	—	6
Glandular with multi-cellular head	V	2	i	6
Glandular with multi-cellular head and multi-cellular base	V	2	ii	6
Peltate	V	3	—	6
Leschenaultia type	V	4	—	6
Dendritic, branched at mid-cell	VI	1	—	7
Dendritic, branched at top of cell	VI	2	—	7
Dendritic, one branch at top and one bottom of cell	VI	3	—	7
Dendritic with very short cells and long arms	VI	4	—	7
Dendritic with unequal arms	VI	5	—	7
Brunonia-type	VII	—	—	7

It is clear once again that Krause's subgeneric divisions have as little bearing on trichome distributions as they have on seed type and inflorescence type (Carolin, 1959, 1966). Little more can be said until a monograph is completed.

In *Scaevola* there are few distinctions, but peltate forms occur in a fairly compact set of species grouped around *S. porocarya*.

In *Dampiera* the only striking grouping of similar trichomes is type IV.5 in Sect. *Camptosperma*.

Acknowledgements

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Bibliography

Carolin, R. C., 1959.—Floral Structure and Anatomy in the family Goodeniaceae. Proc. Linn. Soc. N.S.W., 84 : 282.
————, 1967. The Concept of the Inflorescence in the Order Campanulales. *Ibid.*, 92 : 7.
————, 1966. Seeds and Fruits of the Goodeniaceae. *Ibid.*, 91 : 58.
Colloza, A., 1907, 1908.—Studio anatomico sulle Goodeniaceae, *Nuovo. Giorn. Bot. Ital.*, 14 : 304, 15 : 5.
Hummel, K., 1962. Die Verbreitung der Haartypen in den Naturlichen Verwandtschaftsgruppen. *Encycl. Pflan Anat.*, Berlin.
Krause, K. 1912. Goodeniaceae und Brunoniaceae. *Das Pflanzenreich*, 54, Berlin.
Peacock, W. J., 1963.—Chromosome numbers and cyto-evolution in the Goodeniaceae. Proc. Linn. Soc. N.S.W., 88 : 8.
Uphof, J. C. Th., 1962.—Plant Hairs. *Encycl. Pflan. Anat.*, Berlin.